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Tree rings reveal long-term changes in growth resilience in Southern European riparian forests

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ABSTRACT

The gradual increase in temperature over the last few decades is one of the major consequences of global change. It is also projected that drought frequency and intensity in the Mediterranean region will increase, promoting changes in plant responses to environmental conditions and ultimately species distribution. Studying past growth trends can help understand future impacts of climate change on species-function and predict alterations in how species are distributed. This study sought to evaluate growth trends in riparian tree species to assess both their resistance and resilience responses to, and their complementary strategies in the face of, climatic and hydrological changes. Their supporting ecosystem role in riverine ecosystems and their representativeness in the study region led to the selection of the species *Alnus glutinosa* (L.) Gaertn. and *Fraxinus angustifolia* Vahl for this purpose.

Yearly growth curves were obtained for coexisting *A. glutinosa* and *F. angustifolia*, sampled in 2009 in a riparian forest in a Southern Portuguese river basin. Standardized Precipitation Evapotranspiration Index (SPEI) was calculated to select drought events, identified as years of extreme and severe drought combined with adverse river discharge conditions. Temporal trends in Basal Area Increments (BAI) were explored for both species across 1970–2009, particularly during drought years. Tree growth response was associated with long-term SPEI, minimum temperature, rainfall and discharge.

Both species presented an increase in BAI until the 1980s, apparently triggered by the rise in minimum temperatures, which lengthened the growing season. However, after the 80′s this trend in tree growth has been reversed due to the reduced precipitation associated with increased drought intensity. Similar tree growth responses to drought were observed in both species, but responses to extreme drought events were species-specific. Distinct long-term resilience trends between species suggest that under the current climate change scenario, mesic species (e.g. *A. glutinosa*) will gradually be replaced by more drought-tolerant species, such as *F. angustifolia*.

Finally, further research should be undertaken to provide information on physiological and anatomical changes of riparian tree species in the Mediterranean region.

1. Introduction

The Mediterranean region is said to be one of the most severely affected by climate change, with an increase in temperature and a change in rainfall pattern in the last few decades. These conditions, coupled with predictions by regional climate simulations for the Iberian Peninsula (Spain, Portugal), (IPCC, 2013; Soares et al., 2017; Sumner et al., 2001, 2003) of decreases in rainfall in spring, summer and autumn increase the uncertainty as to how forests will respond to climate change.

Climate change can exacerbate the effect of other stressors, making it difficult to understand plant responses to environmental conditions. Tree species response to climate change has therefore been the object of investigation in recent decades. Peñuelas and Filella (2001) observed an earlier onset of biological spring and a lengthening of the growing season in several species, associating these alterations with global

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warming. Conversely, other studies revealed a decrease in biomass and seedling survival (Garssen et al., 2014), a decline in temperature sensitivity in spring (Fu et al., 2015), and changes in species distribution and relative dominance (Bussotti et al., 2013; Rivaes et al., 2013), all as a result of increasing temperatures. These mixed results show that there are still gaps in our knowledge about the effects of increasing temperature, summer droughts and alteration of waterflow regimes on tree growth and vegetation dynamics. Uncertainty about tree growth responses to projected climate-change scenarios emphasises the need for studies across different time-scales, ecosystems and environmental gradients.

Ongoing climate changes also affect forest stability (Bussotti et al., 2013), testing species' adaptive capacity and their ability to maintain constancy when exposed to those changes (Gunderson, 2000). The impact of ecological disturbances on species growth is often estimated through measures of resistance, recovery and resilience. Resistance is the ability to endure stress conditions without lowering ecological performance. Recovery represents the capacity to recover from the damage suffered during the disturbance (Lloret et al., 2011). Resilience assesses the capacity to recover from disturbances and reach pre-disturbance levels (Gunderson, 2000; Holling, 1986; Lloret et al., 2011). Recently, resistance and resilience indices have been investigated in forest trees to understand their responses to environmental disturbances across species distribution ranges. A combination of the two indices has been used to predict forest composition and species distribution in response to climate changes (Cavin and Jump, 2017; Marqués et al., 2016). In particular, tree species' responses to recurrent extreme events, such as droughts, have revealed changes in resistance and resilience (Gazol and Camarero, 2016; Lloret et al., 2011). Resistance and resilience indices are thus key indicators of the survival of tree species and their acclimatization to climate change (Tatarinov et al., 2016; Trouvé et al., 2017).

As a result of their direct dependence on water and their past degradation, riparian ecosystems display a relatively high level of exposure and sensitivity to changes in climatic conditions, and adaptation presents itself as an opportunity for decreasing their susceptibility to climate change (Capon et al., 2013). Within riparian systems, populations that inhabit the system's rear-edge distribution may play a significant role under current climate change conditions. For example, Hampe and Petit (2005) demonstrated that rear edge populations maintained biodiversity in past periods of climate change, such as glaciations. In Southern Mediterranean riparian corridors, species distribution limits will be affected by increased aridity (Nadal-Sala et al., 2017), notably with changes in tree composition, involving a greater presence of species that are water-stress-tolerant during extreme drought events. Tree growth as an indicator of resistance and resilience to climate change in drought periods could provide new insights on how growth is expected to reflect the changes in tree composition and might help foresee riparian vegetation dynamics after recurrent drought events. In addition, focusing on their current geographic distribution, certain riparian species occurring in the Mediterranean region offer the opportunity to anticipate species responses to future climate conditions.

In Mediterranean riparian corridors, common alder (*Alnus glutinosa*) and narrow-leaved ash (*Fraxinus angustifolia*) are present under a wide range of conditions, from areas with permanent water availability to floodplains with occasional floods. *Alnus glutinosa* is spread throughout most of Europe and exists in a few locations in Northern Africa. Despite the latter, the species' low-latitude limit appears to be southern Europe, where its need for high soil moisture means it can usually be found along river banks (Houston Durrant et al., 2016). The ecology of *A. glutinosa* has been quite comprehensively studied due to its importance as a nitrogen-fixing plant in aiding the river bank stabilization and providing habitat for other plants and animals (Claessens et al., 2010; Heuve, 2011; Vogel et al., 1997). Advancing the study of this species' functional responses to stress would certainly help understand future impacts of emerging global threats to riverine ecosystems such as the *Phytophthora xalni* induced alder decline across Europe (Bjelke et al., 2016). On the other hand, *F. angustifolia* occurs in Southern Europe and Northern Africa, across a wide range of environmental conditions, from high to low altitudes, close to the river or in broadleaved forests (Caudullo and Durrant, 2016). Previous studies in Mediterranean riparian ecosystems have successfully applied dendrochronological methods to both species, when analysing flood impacts and hydrological changes (Ballesteros et al., 2010; Rodríguez-González et al., 2014) and within a range of riparian species (González-Muñoz et al., 2015). Based on the amplitude of the ecological preferences of *A. glutinosa* and *F. angustifolia*, it is therefore expectable that their past growth trends may reveal different responses to climate. This knowledge could help establish management guidelines in riparian restoration projects facing an increasingly uncertain future climate.

This study aims to gain insight into the effect of increased temperature and drought frequency on the temporal changes of tree-growth in *A. glutinosa* and *F. angustifolia* co-occurring in a Mediterranean riparian environment. Based on the ecological preferences of the two species, we hypothesized that 1) the effect of increasing temperatures on growth is positive and similar in both species; 2) tree growth is negatively affected by drought events, but resistance in *F. angustifolia* is mostly determined by climatic factors, whereas responses in *A. glutinosa* growth are modulated by local factors such as river discharge; 3) resilience capacity decreases in both species after recurrent droughts. In order to test these hypotheses, we investigated tree growth temporal patterns in response to increasing temperature and evaluate tree resistance and resilience changes across repeated drought events registered during the second half of the twentieth century.

2. Material and methods

2.1. Study site

The study site was in the Odelouca River (between 37°10′49″N, 8°29′54″W and 37°26′ 33″N, 8°12′16″W), in southern Portugal (Fig. 1). This river belongs to the Arade hydrographic basin and its lithology is mainly composed of alternated layers of schist and greywacke and Mesozoic carbonate rocks (ARH and APA, 2012). It is influenced by two mountain systems with high annual rainfall (from 406 to 1277 mm), mainly in the humid semester, when the climate is predominantly cool and wet (from November to February). The Odelouca River is part of two Special Protection Zones (ZPEs) in the Nature Network 2000 – Monchique, and Caldeirão (PTCON0037 and PTCON0057) – and by the time sampling was performed, was considered as a free-flowing river (APA, 2015).

2.2. Climatic and hydrological data

Monthly climatic data (rainfall, maximum, mean and minimum temperatures) were obtained from the nearest 0.5° × 0.5° grid point in the Climate Research Unit's global gridded database (CRU TS3.10) for the last 100 years (CRU, Harris et al., 2014). The study area is characterized by hot-summer Mediterranean climate according to the Köppen–Geiger classification (ARH and APA, 2012) with marked cool and wet (from November to February), and dry and hot (from May to August) seasons. Temperature and rainfall data were converted to standardised values by subtracting the average for the period 1939-1969. Average daily discharge data were collected for the Odelouca River from the Portuguese Water Resources National Information System (SNIRH) public database (http://snirh.apambiente.pt/index.php?idMain=1&idItem=1.4, last accessed in November 2017). The discharge was converted to standardised values by subtracting the average for 1961 and 1981.

Standardized Precipitation Evapotranspiration Index (SPEI) was calculated for several timescales (to test which period would have a greater impact on water resources), using Potential Evapotranspiration (PET) according to Thornthwaite and estimated with mean temperature

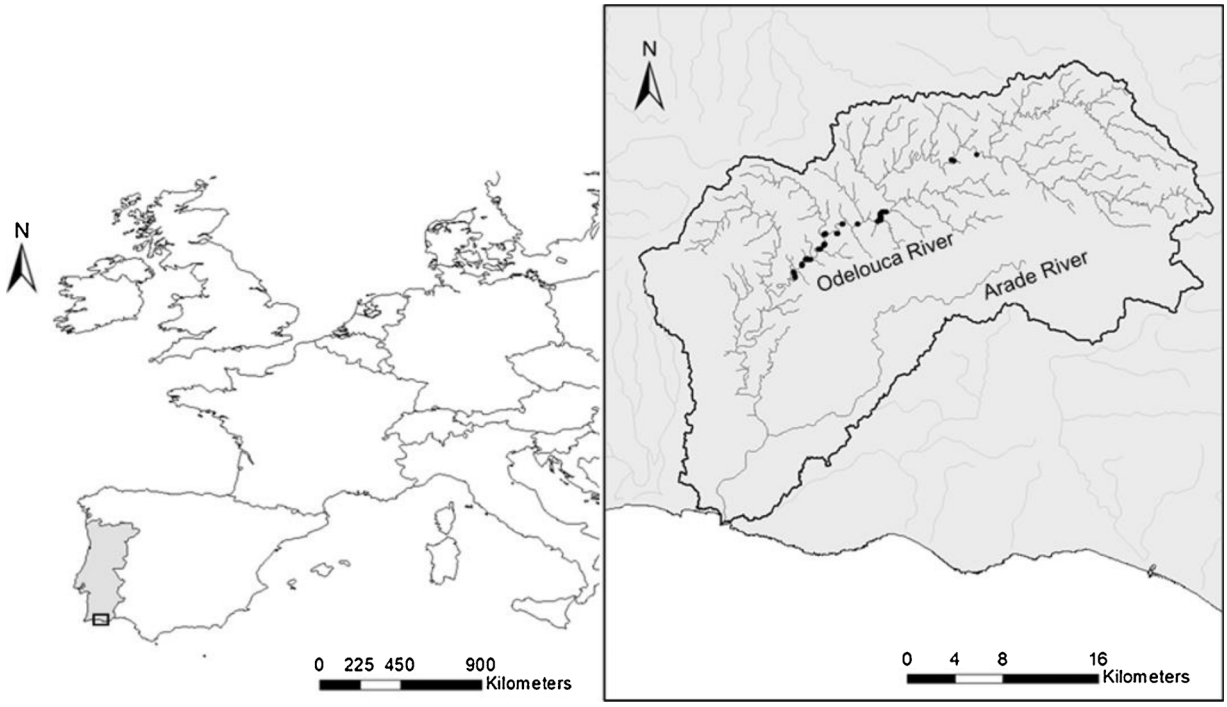

Fig. 1. Study area location in Portugal on the left (black box representing the area were the Odelouca River is located), and sampled trees along the Odelouca River in black dots on the right. Limits of the hydrographic basin are drawn in dark grey line on the right.

and rainfall retrieved for the study area. SPEI is a multi-scalar drought index (Vicente-Serrano et al., 2010), computed to identify drought severity in the study area and selected event years, corresponding to severe and extreme droughts. This index is based on the normalisation of the climatic water balance as the difference between cumulative precipitation and the PET for a given period at monthly intervals. The normalized values of Precipitation-PET (SPEI value) ranges from −3 to 3, and categorize drought events into mild (0 to -0.99), moderate (−1 to −1.49), severe (−1.5 to −1.99) and extreme (≤-2) droughts (Mckee et al., 1993). Both PET and SPEI were calculated using SPEI package (Beguería and Vicente-Serrano, 2013) for R program version 3.4.3 (R Development Core Team, 2016). We estimated the SPEI for different time scales (from 3 months to 12 months) and selected the one that best identified the severe droughts for the Odelouca area, derived from climatic and historical data.

All the analysis of climatic and hydrological data were performed for the period between 1970 and 2009.

2.3. Dendrochronological analysis

Fieldwork was conducted in the summer of 2009 along a 37 km reach of the Odelouca River. Before the dendrochronological sampling, in sites where both species were present along the selected reach, trees larger than 20 cm were georeferenced, labeled and measured. Then, 75 trees of each species were randomly selected in order to obtain a balanced distribution of trees, longitudinally along the reach and transversally across habitats (channel, bank and floodplain). Trees with rotten stems were excluded so that a total of 72 *F. angustifolia* trees and 61 *A. glutinosa* trees were considered. At least 2 samples were collected by individual either from stem disks or using an increment borer with 5 mm of diameter at the breast height (1.30 m). Samples were subsequently mounted on wood supports, dried and their surfaces sanded up to 400grit sandpaper. Tree-ring widths were measured with an accuracy of 0.01 mm on a LINTAB digital positioning table connected to the software TSAP (Rinntech, Heidelberg, Germany). Individual tree-ring series were visually cross-dated and statistically verified using TSAP and the detrendeR package (Campelo 2012) in R program version 3.4.3 (R Development Core Team, 2016). Trees with less than 20 tree-rings or a correlation with the mean of less than 0.25 were discarded from further analysis. Considering these criteria, from the initial 133 trees only 69 were included in the analysis, comprising a total of 150 radii (87 radii representing 39 *F. angustifolia* individuals and 63 radii representing 30 *A. glutinosa* individuals). In addition, all selected series presented correlations above 0.4 after detrending.

Chronologies were developed for both species with the dplR (Bunn, 2010, 2008; Bunn et al., 2018) and detrendeR (Campelo et al., 2012) packages, by fitting a smoothing spline of 30-year wavelength and a response of 0.5 to each tree-ring series. An auto-regressive model was applied to each ring-index series and the resulting series were used to compute the residual chronology. The Expressed Population Signal (EPS) was calculated to estimate how well the resulting chronology represented the signal of a perfect chronology (i.e., an infinitely replicated chronology) (Briffa and Jones, 1990; Wigley et al., 1984). Following Wigley et al., (1984), the subsample signal strength (SSS) was used with a threshold value of 0.85 to determine the period for which the chronology was sufficiently replicated to be considered reliable.

Radial growth was expressed as yearly Basal Area Increment (BAI), calculated by converting the ring-width series to ring-area series based on the distance between the outermost measured ring of the tree and the pith. This method assumes a concentric circularity. In order to decrease the effect of eccentric growth - common in these species - BAI was calculated using the mean of all radii per tree. The distance to the pith, when present, was measured directly from the wood samples, excluding bark. In samples without the pith, the circular method was used to estimate the distance to pith (Campelo et al., 2013; Liu, 1986). This method relies on calculating the average ring width of the innermost rings of all samples with pith, for each tree species. BAI was calculated for the period 1932–2009 to guarantee that at least five cores were used per year, using bai.in function of dplR package (Bunn, 2010, 2008; Bunn et al., 2018). In order to minimize age-effect, only tree-ring series above 20 years and below 77 years were used. As such, 36 and 30 trees were used to calculate BAI for *F. angustifolia* and *A. glutinosa*, respectively.

Resistance and resilience indices were calculated for each species in order to evaluate response to drought events, according to definitions established by Lloret et al. (2011). Lloret et al. (2011) define resistance as the "reversal of the reduction in ecological performance during disturbance" and say it can be estimated as "the ratio between the performance during and before the disturbance". The same authors consider that resilience reflects "the capacity to reach pre-disturbance performance levels" and can be calculated as the "ratio between the performance after and before disturbance". These indices were calculated using raw tree-ring widths and BAI data, with 3 years of pre- and post-disturbance (Gazol et al., 2017; Pretzsch et al., 2013). Resistance and resilience were calculated according to the method proposed by Lloret et al. (2011). Resistance was calculated using the equation $Rt = Dr/PreDr$, where Rt is the resistance, Dr is the growth during the drought and $PreDr$ is the growth before the drought period. Resilience was calculated with the equation $Rs = PostDr/PreDr$, where Rs is the resilience and $PostDr$ is the growth after the drought period. The PointRes R package was used to compute these indices (van der Maaten-Theunissen et al., 2015).

To analyse the effect of environmental conditions on tree growth, the resistance and resilience indices were correlated with monthly values of SPEI, rainfall, minimum temperature and discharge using Pearson correlations. The correlations were calculated for a 36-years period (1970–2005). We conducted a factorial analysis of variance (ANOVA) with resilience and resistance indices as dependent variables, and species as independent variables. No violation of the ANOVA assumptions (normality of residuals, homogeneity of variances) was found after data testing. This analysis was for the selected drought events, and Fisher's post-hoc tests were used to compare the different levels of the independent variables.

3. Results

3.1. Climate trends

Annual temperature standardised values in the Odelouca region have increased since 1900, while the amplitude of the range between minimum and maximum temperatures has decreased (Fig. 2a). Maximum temperature was the most affected by recent climate evolution in the Odelouca area, with an apparent increase since 1970 and peak values in 1995 and 2014. Changes in minimum temperature followed maximum temperature trends until 2000.

There was no obvious trend in rainfall in 1970–2009 (Fig. 2b). Minimum rainfall standardized values were found in 1974, 1981, 1994, 1998 and 2005. Negative standardized values had been more frequent and lower in value since the 1970s, coinciding with a decrease in the range between maximum and minimum temperatures and an increase in positive standardized values.

There was a decrease in maximum discharge values in the data for the first 15 years (1960–1975), followed by an increase on the following 30 years (Fig. 2c). The highest value in 1960–2009 was in 1996, closely followed by the year 1989. Lower discharge values were visible for continuous periods of 2–4 years, followed and preceded by rapid increases in discharge.

After comparing climatic data and historical reports, a timescale of 7 months was chosen to calculate SPEI. Drought events have been increasingly more intense and prolonged since 1950, with a higher frequency from 1969 to 2009 (Fig. 3). Longer periods with negative SPEI in summer months were found in several years (e.g. 1981, 1983, 1985,

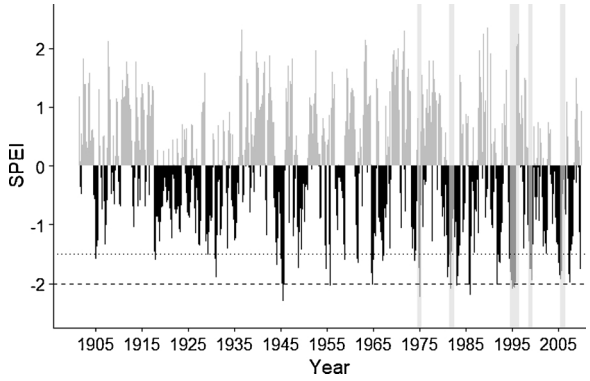

Fig. 3. Standardized Precipitation Evapotranspiration Index (SPEI) for 7-month scale, for the Odelouca area. The SPEI includes the standardized water balance (calculated from monthly differences between precipitation and Potential Evapotranspiration) for the 7 previous months. Selected drought events (1974, 1981, 1994, 1995, 1998 and 2005) are highlighted in grey. Severe drought threshold is identified by a dotted line and extreme drought threshold by a dashed line, both in the negative area of the y-axis.

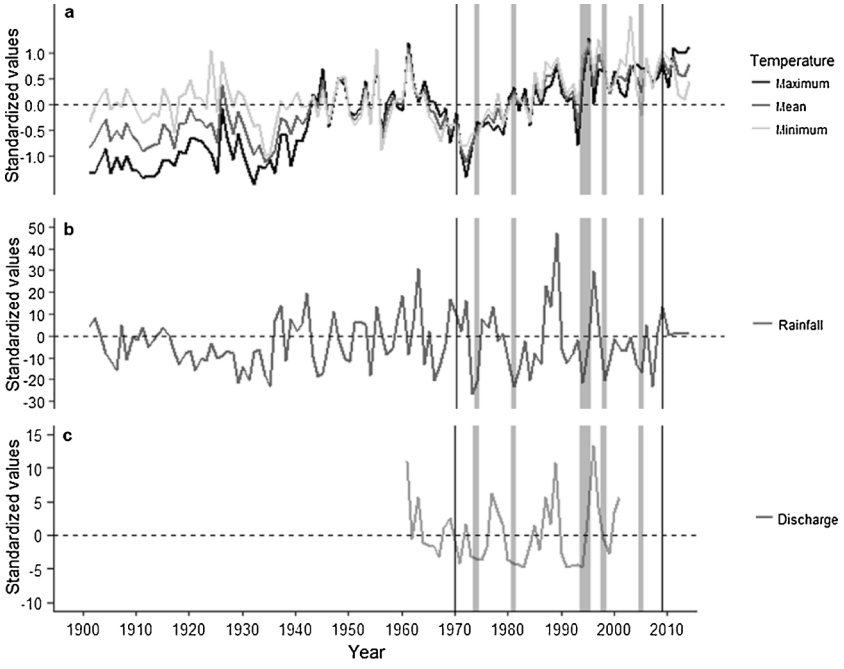

Fig. 2. Temperature standardized values (maximum, mean and minimum temperatures) – a, rainfall standardized values - b and discharge standardized values - c. The area delimited by vertical lines represents the studied period between 1970–2009. Grey areas identify drought events selected for this study (1974, 1981, 1994, 1995, 1998 and 2005).

1994, 1995, 1999, 2004 and 2005), corresponding to periods that presented greater evapotranspiration and were drier than average.

Years with low amounts of rainfall and discharge combined with high temperature standardized values were identified as possible stressors for tree growth. The identified years (1973, 1974, 1980, 1981, 1985, 1992, 1994, 1995, 1998 and 1999) were later cross-referenced with years presenting SPEI values below -1.5, i.e., only those with severe and extreme drought events. The last selected drought events occurred in 1974, 1981, 1994, 1995, 1998 and 2005 (Fig. 3), coinciding with years with higher temperatures (minimum and maximum) that were either preceded by or experienced lower rainfall. Also, combining all information, 1981, 1995 and 2005 were considered the years with the greatest possible repercussions for tree growth in the studied area. In the 1981 and 2005 events, drought conditions lasted the whole year and were preceded by 4 months of extreme drought (< -1.5). In the 1995 drought event, extreme drought conditions persisted for more than half the year (8 months).

3.2. Growth patterns and climate-growth relationships

The chronology covered 119 years (1891–2009) for *F. angustifolia* and 67 years (1943–2009) for *A. glutinosa* (Fig. A.1 in the Supplementary material). The common interval used for further analysis of both species, selected by the EPS and SSS values (Table 1), was between 1970 and 2009.

Results showed similar growth patterns for both species starting in 1940, with a steeper increase between 1970 and 1990 (Fig. 4). During this period, BAI increased, reaching maximum values for the entire analysed period (4393 mm^2 for *F. angustifolia* in 1990 and 3647 mm^2 for *A. glutinosa* in 1988). This increase was followed by a steep decrease until 2009, reaching area values that were similar to those for 1970, when the increase in the basal area began. When the 32-year spline fitted to BAI values was analysed, low peaks were found for both species in 1981 and 2005. The difference in BAI between *F. angustifolia* and *A. glutinosa* was more noticeable in 1974, 1991, and between 1996 and 2009 (except for 2005).

During the timespan selected for analysis, tree-ring width index reached its maximum in 2009 for *A. glutinosa* and in 1990 for *F. angustifolia* (1.28 and 1.29, respectively) (Fig. A.1 in the Supplementary material). Both species presented low tree-ring growth rates in 1981, 1984, 1997 and 2000 and high tree-ring growth in 1985. The lowest ring-width index for *A. glutinosa* was in 1996, which coincided with a flash flood event in Odelouca River, close to the 100-year return period

Table 1
Dendrochronological data for *Alnus glutinosa* and *Fraxinus angustifolia*. EPS – Expressed Population Signal; SSS – Subsample Signal Strength (with threshold of 0.85).

	F. angustifolia	*A. glutinosa*
Chronology length	1891–2009	1943–2009
Number of trees	39	30
Number of cores	87	63
Mean tree-ring width	4.1	4.15
Mean correlation:		
among all radii	0.37	0.23
between trees	0.37	0.22
within trees	0.81	0.52
Common interval (1978-2009)		
Number of trees	27	22
Number of cores	64	48
EPS	0.89	0.87
Mean correlation:		
among all radii	0.22	0.2
between trees	0.21	0.19
within trees	0.73	0.5
Interval (SSS > 0.85)	1938–2009	1958–2009

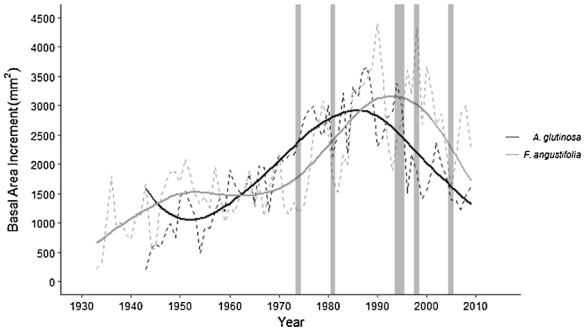

Fig. 4. Basal Area Increment (BAI) chronologies (dashed line) for both species, *F. angustifolia* in grey and *A. glutinosa* in black. Continuous lines are 32 years spline calculated from BAI values. Grey areas identify drought events selected for this study.

discharge for this drainage basin (Rivaes et al., 2013; Rodríguez-González et al., 2014). In general, *F. angustifolia* presented a smaller range between maximum and minimum ring width values than *A. glutinosa*. Both species displayed narrow tree-rings in extreme droughts events (e.g. 1981 and 2005).

3.3. Tree resistance and resilience

Even though studied trees were growing in the study area under a range of similar environmental conditions, the response of the two species to drought events was usually distinct, although a similar behaviour was noticeable in the case of one such event. The last 40 years presented an opposite evolution in resistance and resilience between species (Fig. 5). In general, resistance and resilience indices calculated from tree-ring width (Fig. B.1 in the Supplementary material) presented similar correlation results to those obtained from BAI resistance and resilience (Fig. 6).

Across species, *A. glutinosa* revealed itself more capable of maintaining stable growth before, during, and after drought events (resistance and resilience), when compared with *F. angustifolia* (BAI = in Fig. 5a and b; raw tree ring-width = in Fig. B.1a and b in the Supplementary material). The range between maximum and minimum resilience values has been decreasing since the beginning of the studied period for *F. angustifolia*, while *A. glutinosa* has maintained a relatively constant resilience over the last few decades. Having said this, resilience was typically greater for *F. angustifolia*.

When only the selected drought events were analysed, *F. angustifolia* and *A. glutinosa* presented similar values for both resistance and resilience in the 1998 drought. For the remaining selected drought events, *F. angustifolia*'s resilience values were higher than its resistance values; whereas *A. glutinosa* displayed a decrease in resilience in the rest of the most recent drought events (resistance was higher or close to resilience in 1994, 1995 and 2005: resistance 1.17, 0.97, 0.62 and resilience 0.75, 0.56 and 0.63 respectively).

A similar temporal pattern of increasing (e.g. maximum values) and decreasing (e.g. minimum values) resistance and resilience was observed before the 1980s for both species. This pattern was more evident for resistance calculated from both BAI and ring-width index. In the case of resistance (ring-width index), both species present a maximum value in 1970 (1.21 for *A. glutinosa* and 1.15 for *F. angustifolia*), followed by a minimum value between 1971 and 1977/1978 (0.86 in *A. glutinosa in 1974* and 0.6 in *F. angustifolia* in 1972) and then again, attaining maximum values in 1977 for *A. glutinosa* – 1.1 and *F. angustifolia* – 1.33). The same is true of the BAI resistance values, with a fall in 1974 for *A. glutinosa* and in 1972 in *F. angustifolia*. A maximum occurs in 1977 in *A. glutinosa* and in 1978 in *F. angustifolia*. For both resistance indices (BAI and ring-width), minimum values occur again in 1981 (BAI = 0.71 for *A. glutinosa* and 0.7 for *F. angustifolia*; tree ring

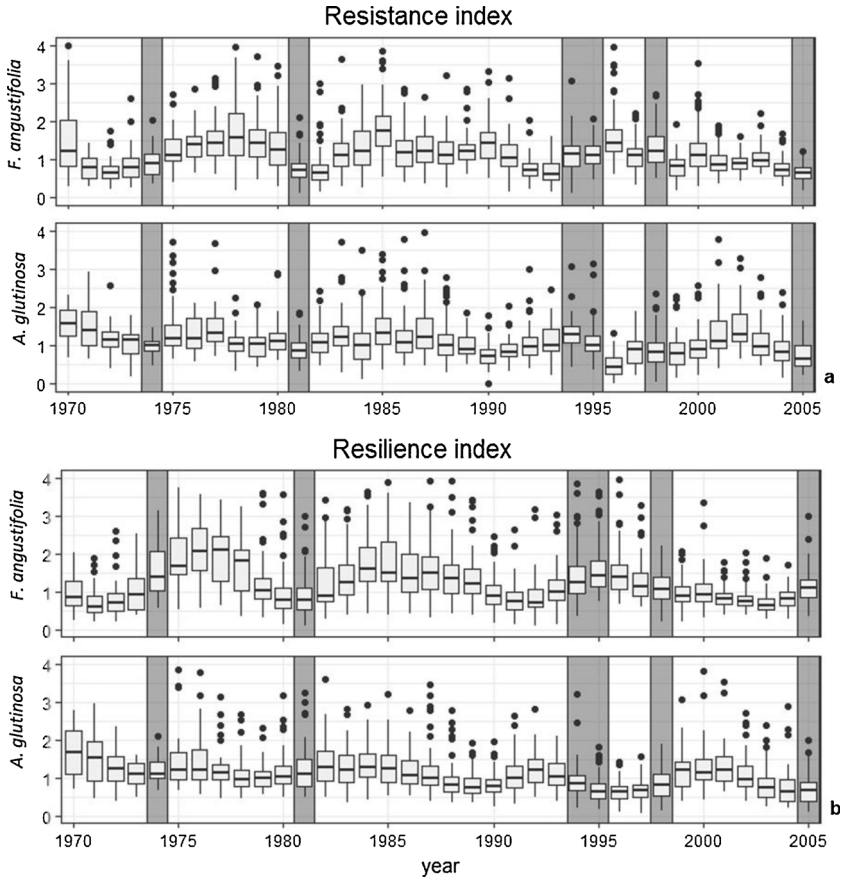

Fig. 5. Resistance index calculated from BAI for *Alnus glutinosa* and *Fraxinus angustifolia* with drought events highlighted in grey - a. Resilience index calculated from BAI for *Alnus glutinosa* and *Fraxinus angustifolia* with drought events highlighted in grey - b.

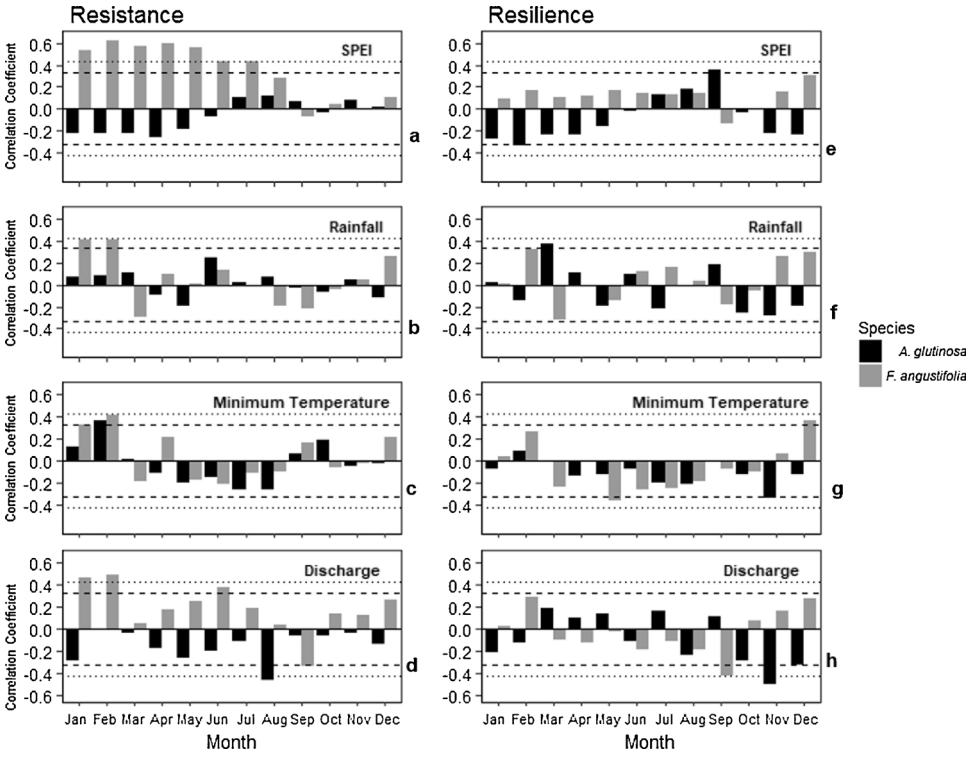

Fig. 6. Correlations between Resistance index and SPEI (a), Rainfall (b), Minimum Temperature (c), Discharge (d); between Resilience index and SPEI (e), Rainfall (f), Minimum Temperature (g) and Discharge (h). Significance levels of $p < 0.05$ are identified by dashed lines and levels of $p < 0.01$ by dotted lines. Resistance and resilience indices were calculated using BAI (Basal Area Increment).

width = 0.71 for *A. glutinosa* and 0.62 for *F. angustifolia*). After this, a time lag of up to 3 years was present between species in the temporal pattern of increasing and decreasing values (Fig. 5a and b). In the case of ring-width index resistance, the minimum values of 1981 were followed by a peak for both species in 1985 (1.135 for *A. glutinosa* and 1.53 for *F. angustifolia*) and then minimum values 5 years (1990 for *A. glutinosa*) and 8 years (1993 for *F. angustifolia*) later. This difference persisted in the next minimum values - in 1996 for *A. glutinosa* and 1999 for *F. angustifolia*. A similar situation was observed for BAI resistance. This situation matched the extreme drought event of 1981, which may have had some effect on species-specific response.

When comparing temporal trends between drought events, it was possible to distinguish behaviours between species mediated by drought severity. More severe drought events in 1974, 1981 and 2005 corresponded to a decrease in resistance values for both species, reaching the minimum value (for BAI) of 0.65 for *F. angustifolia* and 0.62 for *A. glutinosa* in 2005. However, this common behaviour did not apply to the less severe drought events of 1994, 1995 and 1998. In general, *A. glutinosa* decreased its growth effort (resistance reduced from 0.86 in 1974 to 0.62 in 2005, and resilience from 0.98 in 1974 to 0.635 in 2005). During drought events, there seemed to be no visible trend for resilience in *F. angustifolia*.

Comparing species response for each component per drought event, we found it to be significant in terms of resistance for the 1994, 1998 and 2005 drought events and with regard to resilience for the 1974, 1994, 1995 (only in BAI), 1998 and 2005 events (ANOVA measures, $p < 0.05$) (BAI = Table 2; raw ring-width = Table B.1 in the supplementary material). Both species presented an identical response for both resistance and resilience during the 1981 drought event. Resilience was more influenced by species-specific response than resistance was. Where resistance was concerned, only 1994 and 1998 drought events - two of the less severe events - presented a species-specific response.

SPEI was the climatic variable with the greatest impact on *F. angustifolia* resistance, during the first months of the year (BAI = Fig. 6a; raw ring-width = Fig. B.2a in the supplementary material). This shows that drought conditions in spring and summer were especially influential for *F. angustifolia* resistance. Additionally, resistance in *F. angustifolia* presented positive correlations with rainfall, minimum temperatures and discharge in the early part of the year (January and February) (BAI = Fig. 6b–d; raw ring-width = Fig. B.2–d in the Supplementary material). Similarly, significant negative correlations were observed between September discharge and resistance in *F. angustifolia* (BAI = Fig. 6h).

Resilience showed a greater number of significant correlations with minimum temperature, but more significant correlations with discharge and in overall, resilience was not correlated with monthly climatic variables to any great extent. The only positive effects on resilience were for rainfall in March for *A. glutinosa* and minimum temperature in December for *F. angustifolia* (BAI = in Fig. 6f and g; raw tree ring-width = Fig. B.2f and g in Supplementary material). Negative effects occurred in May and November minimum temperatures (for *F. angustifolia* and *A. glutinosa*, respectively), and in September discharge (*F. angustifolia*) and November discharge (*A. glutinosa*) (BAI = in Fig. 6g and h; raw tree ring-width = in Fig. B.2g and h in the Supplementary material).

Resistance and resilience *in A. glutinosa* presented fewer significant correlations with climatic variables than *F. angustifolia*. Resistance in *A. glutinosa* was negatively correlated to August discharge (BAI = Fig. 6d; raw ring-width = Fig. B.2d in the Supplementary material), and positively correlated with minimum temperature in February (BAI = Fig. 6c; raw ring-width = Fig. B.2c in the Supplementary material). Resilience in *A. glutinosa* appears more dependent than resistance on climatic conditions. Moreover, climatic conditions in March (high rainfall), and September (high SPEI) enhanced resilience for *A. glutinosa* (BAI = Fig. 6e and f; raw ring-width = Fig. B.2e and f in the Supplementary material), while November discharge reduced resilience (BAI = Fig. 6h; raw ring-width = Fig. B.2h in the Supplementary material).

Table 2
Analysis of variance for species effect on resistance and resilience, calculated from BAI, for drought events (1974, 1981, 1994, 1995, 1998 and 2005). DF – Degrees of Freedom; SS – Sum of Squares; MS – Mean square; F – *F-statistics*. Years with p-value in bold are significant ($p < 0.05$).

Source	*Drought Event*	*DF*	*SS*	*MS*	*F*	*p-value*
		Resistance				
Species	1974	1	0.019	0.019	0.154	0.696
Residuals		76	9.185	0.121		
Species	1981	1	0.064	0.064	0.575	0.45
Residuals		103	11.411	0.111		
Species	1994	1	2.028	2.028	12.893	< **0.001**
Residuals		138	21.701	0.157		
Species	1995	1	0.057	0.057	0.423	0.5164
Residuals		139	18.791	0.136		
Species	1998	1	8.623	8.683	50.77	< **0.001**
Residuals		137	23.43	0.171		
Species	2005	1	0.347	0.346	3.713	0.056
Residuals		140	13.063	0.093		
		Resilience				
Species	1974	1	2.92	2.921	15.988	< **0.001**
Residuals		69	12.606	0.183		
Species	1981	1	0.027	0.027	0.189	0.664
Residuals		98	13.956	0.142		
Species	1994	1	4.486	4.486	33.839	< **0.001**
Residuals		130	17.234	0.131		
Species	1995	1	13.547	13.547	103.39	< **0.001**
Residuals		133	17.425	0.131		
Species	1998	1	5.108	5.108	29.993	< **0.001**
Residuals		140	23.842	0.171		
Species	2005	1	4.33	4.33	34.511	< **0.001**
		138	17.314	0.126		

4. Discussion

4.1. Average climate effects on tree growth

The Mediterranean region is projected to be among the areas that will be most severely affected by climate change, with an increase in temperature and water stress, especially during the warm season (April to September) (Giorgi, 2006; Giorgi and Lionello, 2008). As far as we know, this study represents the first attempt at deciphering the relationship between resistance, resilience and tree growth responses to drought events for riparian species with different ecological strategies. Similar to what has happened across whole southern Europe, environmental conditions in the Odelouca River have been changing mostly since the 1970s. The observed increase in maximum and minimum temperatures, associated with a greater variability in rainfall and an increase in drought frequency and severity, could alter the response of tree species to climate. Our results supported the initial hypothesis that current climate warming promotes tree-ring growth for both species. However, this response was not maintained throughout the entire studied period.

We observed a persistent increase in basal area increment from 1960 to 1980s (in *A. glutinosa*) and 1990s (in *F. angustifolia*), which coincided with the increase in the minimum temperatures in the study area. Warmer conditions at the end of the growing season allow its extension, provided water availability is not a limiting factor. These conditions fostered positive growth responses for some decades between 1960 to 1990, corroborating evidence that suggests positive correlations between temperature and phenological changes (Peñuelas and Filella, 2001), an increase in tree-ring width during the last few decades for upland species (Tegel et al., 2014), and an increase in radial growth for *F. angustifolia* (González-Muñoz et al., 2015) in a riparian environment in Spain. However, both species presented a steep decrease in tree growth, beginning between mid-1980s to mid-1990s,

while the amplitude of the variations in tree-ring width decreased, presenting lower maximum values. The decrease in growth suggests that the cumulative effect of climatic factors (temperature, drought and rainfall) forced a threshold, after which incremental growth response was no longer visible, but instead there was a decrease in growth capacity. A similar result was obtained for *Fagus sylvatica* L. in Spain (Jump et al., 2006). The growth decrease observed for both species in the present study shows that climatic conditions are a common limiting factor for growth, despite greater water availability for *A. glutinosa*.

4.2. Short-term effects of drought events across species

Resistance and resilience indices calculated in this study are used to discuss tree-growth responses to stressful environmental conditions, such as drought and increasing temperatures, in co-occurring populations of *F. angustifolia and A. glutinosa*. This novel approach allowed us to detect complementarity in tree-growth trends between the two species. For the whole of the period under analysis, when *F. angustifolia* invested in resilience, *A. glutinosa* presented high resistance values (in years 1974–1975, 1985–1988, 1994–1995), while the analysis of long-term regional and local effects on tree growth suggests a difference in species responses.

Our initial hypothesis was that growth would be negatively influenced by drought recurrence in both species, but that the studied indices (resistance and resilience) would reflect a different trend in each species, due to their respective ecological preferences. As expected, the results showed that the ability to reach pre-drought growth levels (resilience) was more closely related to local environmental conditions (discharge) in *A. glutinosa*, whereas *F. angustifolia* presented a higher number of significant responses to regional climatic stressors (in May and December minimum temperatures).

Climatic conditions influenced resilience less than resistance for both species, even though all the analysed variables (SPEI, rainfall, minimum temperature, and discharge) were significantly correlated with both resistance and resilience (Fig. 6). The higher number of significant correlations of climatic variables and resistance, mostly occurring in *F. angustifolia*, suggests that environmental conditions in previous years are a determining factor in the ability of trees to overcome the negative effects of drought on growth - something that has been referred to as “ecological memory” (Johnstone et al., 2016). *A. glutinosa* also showed a positive response on the resistance and resilience of stressful conditions, such as the lower discharge in late summer and autumn. A significant positive correlation between resistance and discharge in winter (January and February) and spring (June) for *F. angustifolia* could be related to the replenishment of river flow and water reserves, thus allowing trees to sustain drought events.

Drought impact on trees depends on the timescales of the drought (Vicente-Serrano et al., 2013), according to the trees’ capacity to withstand water deficits. Greater water availability and geomorphic position are important features for *A. glutinosa* distribution within fluvial systems. These conditions restricted the presence of this species to a downstream section of Odelouca River with a relatively large drainage basin area and hence a higher average discharge than that in upstream reaches (Rodríguez-González et al., 2014). This would explain why, compared with *F. angustifolia*, *A. glutinosa*’s resistance and resilience presented more significant correlations for discharge but lower significant correlations with climatic variables. For *F. angustifolia,* the high correlation between resistance and SPEI indicates the strong effect of drought on tree growth during summer and autumn months. Better conditions and accumulated resources during part of the dry season (e.g. rainfall and humidity from April to October) promoted resistance (growth maintenance between years during and before drought events). Similarly, in this species resistance was enhanced by water availability during late winter and early spring. This was expected for *F. angustifolia* due to its position farther from the river and thus its more limited access to water. On the one hand, *F. angustifolia* displayed greater resistance in severe droughts, probably due to its better adaptation to the need to withstand aridity compared to *A. glutinosa*. On the other hand, lower discharge values had the greatest impact on resistance and resilience response of *A. glutinosa.*

In a riparian environment, there is a marked transversal gradient in terms of water availability and hydrological disturbance that runs from the channel, through the floodplains and up to the upland forest. The distinct ecological needs of *A. glutinosa* and *F. angustifolia* were evident when analysing the environmental factors that could modulate species response and the species’ strategies in the face of drought. For instance, the resistance response to severe drought was of a stand-level nature, while resilience was mainly species-specific. Regardless of local conditions, the response to the extreme drought of 1981 was shared between species. Accordingly, studies have shown that there could be a community-dependent response regarding species composition to very severe droughts (Urbina et al., 2015). Also, species-specific drought vulnerability was found when species were subjected to a continuous moderate and episodic severe drought in a Mediterranean forest (Liu et al., 2015). Contrary to the trend, the extreme drought events of 1995 and 2005 did not reveal a common behaviour between species and between resistance and resilience indices. This may be because neither event attained the harshness of the conditions of 1981 (e.g. longest period of low river discharge and the second lowest rainfall anomaly). High temperatures associated with low water availability attained such a minimum in 1981 that trees started reducing their growth during and after the drought event, in order to be able to survive. Interestingly, there was a more pronounced decrease in basal increment in the next extreme drought (1995), suggesting a cumulative stress effect. The similar behaviour displayed by both species with regard to resistance and resilience during the extreme drought event of 1981 seems to correspond to the beginning of the inflection point observed in basal area increment, which then became pronounced from 1990 onwards (Fig. 4).

4.3. Long-term effects of severe and extreme events across species

The studied populations occur at the rear-edge of their distribution, exposed to sub-optimal environmental conditions. We therefore hypothesized a decrease in resilience for both species, due to an increase in drought events and progressive harsher climatic conditions. This was noticeable for *F. angustifolia*, which decreased the amplitude of its resilience index across the studied period, but not for *A. glutinosa*, whose resistance and resilience indices were maintained. The second type of response - i.e., resilience unaffected by past low-growth periods and no decrease over time has been observed in a ponderosa pine/Douglas-fir forest (Lloret et al., 2011).

As expected, SPEI offered the best response among the studied variables, probably due to the integration of different climate conditions (temperature, rainfall and evapotranspiration) in a single variable. On the other hand, the lack of significant correlations in rainfall and minimum temperature for both species, was unexpected, indicating that drought intensity and severity was the most important factor controlling tree growth response to climate change.

Local hydrology conditions were essential for *A. glutinosa* tree growth, in line with its spatial distribution closer to the river and its relative protection from high temperatures and water stress – a typical feature of a wetland tree (Rodríguez-González et al., 2010). The suitable ecological environment for the *A. glutinosa* studied in this river may explain the maintenance of relatively constant resistance and resilience values during the initial decades of the studied period. However, the later decades displayed increasing fluctuations in the return to pre-drought growth levels, possibly due to the increase in local stressful conditions, such as lower discharges during late summer and early winter. This might also indicate a change in the trees’ strategies in the face of drought events. We should note that this study was limited to trees that survived to drought events, and it was not possible to examine these indices for trees that died due to climatic stress. As a result,

the analysed tree samples may present some degree of adjustment in response to harsh climate conditions. A complementary analysis of the causes of tree mortality in the population would help validate assumptions of resilience maintenance for *A. glutinosa*.

Conversely, *F. angustifolia,* trees show shallow root systems and are, often located further from the river (Sánchez-Pérez et al., 2008; Singer et al., 2014, 2012). Thus, after an increase in drought severity, *F. angustifolia* individuals were unable to return to pre-drought growth rates, resulting in a reduction in resilience.

Our results suggest that current climate changes could affect species distribution in riparian corridors, with the gradual replacement of more water-demanding species, such as *A. glutinosa*, by more drought-tolerant ones (Garssen et al., 2014; Ikeda et al., 2014; Nadal-Sala et al., 2017). Greater water stress for riparian trees can lead to higher competition for water resources between individuals, compromising their future coexistence (Granda et al., 2013). In the studied environments, the composition might shift towards *F. angustifolia* (Singer et al., 2012), as it is better adapted to variable water source conditions. However, in a study with grassland and heath, mild droughts over time have been linked to an increase in resistance to extreme drought events (Backhaus et al., 2014). The increase in resistance observed in *F. angustifolia* supports the hypothesis that this species could supersede *A. glutinosa* in terms of its position in this river. However, the maintenance of resilience for *A. glutinosa*, as opposed to the decrease for *F. angustifolia*, could be consistent with an acclimation of tree species to a warmer environment, with higher temperatures and lower rainfall and discharge.

4.4. Implications for the dynamics of riparian trees distribution

Adaptive forest strategies in response to environmental changes can include persistence of the current tree mechanisms or species substitution (Bussotti et al., 2015). Even though results suggest future changes in tree distribution along riverine ecosystems, where the replacement of riparian species by xeric species can be expected in a climate-warming scenario (Rivaes et al., 2013; Ström et al., 2012) we do not exclude the possibility of tree adaptation. The potential species resilience to global changes and the positive forest responses observed as a result of measures to mitigate human effects on waterflow regimes (Rodríguez-González et al., 2017) point out the possible adaptation of these sensitive ecosystems.

By studying two co-occurring species we were able to depict the complementary growth strategies, illustrated by long-term resistance and resilience tree-growth dynamics in a small Mediterranean river in Southern Europe. The studied area was particularly important due to its near-pristine conditions, enabling us to characterise the dynamics of these species and tree-growth responses in a close-to-natural system presenting limited anthropic intervention. This could help to shed light on the possible responses of natural riverine vegetation to climate change and provide clues for the upscaling of our field data from the tree population to the ecosystem level in a scenario of species dominance shift.

Future research should focus on the underlying causes of vegetation response to drought events and on how different tree species will respond to more frequent and intense droughts in river corridors. More knowledge about the specific features of tree species, including anatomical and physiologic traits, will help understand the mechanisms that regulate the response of trees to drought in the Mediterranean riparian corridors. This will, in turn, permit better management decisions, favouring the persistence of the ecological and functional diversity of these valuable ecosystems.

Competing interests

The authors have declared that no competing interests exist.

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Appendix A. Supplementary data

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